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EXAMINING WHOOPING CRANE BREEDING SEASON FORAGING BEHAVIOR IN THE EASTERN MIGRATORY POPULATION

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Abstract: Agricultural fields may provide an important supplementary foraging habitat for whooping cranes (*Grus americana*) in the reintroduced Eastern Migratory Population (EMP). We developed methods and gathered preliminary data regarding whooping crane foraging efficiency and habitat use to better understand the use of agricultural fields by breeding cranes. We generated a simple null hypothesis that cranes would spend more time in the habitat type (wetlands vs. agricultural fields) in which they were able to obtain a higher foraging efficiency to maximize food intake, along with several alternative hypotheses pertaining to reasons cranes may prefer wetlands or agricultural fields during periods of the breeding season regardless of foraging efficiency. We collected habitat use and measures of foraging efficiency (stepping rate, striking efficiency, and capture rate) from videos of 2 pairs of cranes recorded for a concurrent study. Cranes spent more time in the habitat with higher foraging efficiency during the pre-nesting period (wetlands) but more time in the habitat with lower foraging efficiency during the incubation period (also wetlands). There was no significant difference in foraging efficiency post nest-abandonment. Our data imply that cranes are willing to undergo lower foraging efficiencies in order to remain on territory during incubation. However, our data should be considered preliminary due to the small sample size of individuals studied.

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Key words: feeding behavior, *Grus americana*, habitat use, species reintroduction, whooping crane, Wisconsin.

Breeding pairs of whooping cranes (*Grus americana*) in the reintroduced Eastern Migratory Population (EMP) display different habitat use patterns from breeding cranes in the extant wild Aransas-Wood Buffalo Population (AWBP) (Barzen 2018). Though both populations show a preference for emergent herbaceous wetlands in their nesting territories, whooping cranes in the EMP also use agricultural fields, a habitat type not found near the breeding grounds of the AWBP. These agricultural areas are generally not adjacent to, and can be far away from (e.g., 10-15 km; Fitzpatrick 2016, Barzen et al. 2018c), the nesting territories and may be used daily by nesting cranes (Van Schmidt et al. 2014). Van Schmidt et al. (2014) proposed that agricultural fields could be an important supplemental foraging habitat for EMP cranes.

EMP cranes have been observed to make particularly heavy use of off-territory agricultural areas after nest abandonment (Van Schmidt et al. 2014, Fitzpatrick 2016). A high rate of nest abandonment is 1 of the primary causes of the population's low reproductive success (Urbanek et al. 2014, Whooping Crane Eastern Partnership 2014). Nest abandonments are caused

primarily by harassment from avian-feeding black flies (*Simulium* spp.; Converse et al. 2013, King et al. 2013, Barzen et al. 2018a). However, the pattern of widespread use of off-territory agricultural fields during nesting and following abandonment (Van Schmidt et al. 2014) could be an indication that low food availability on nesting territories contributes to nest abandonment, in combination with stress caused by black fly parasitism.

Study of the factors underlying such habitat use by EMP cranes would improve understanding of habitat requirements in the context of the nesting cycle and black fly parasitism. Previous studies of the EMP have examined aspects of breeding season habitat use and selection (Maguire 2008, Van Schmidt et al. 2014) and foraging behavior and energetics (Fitzpatrick 2016, Barzen et al. 2018d). However, the only other study providing whooping crane foraging efficiency metrics in relation to habitat use was conducted on the wintering grounds of the AWBP, where winter habitat use fluctuated over the course of the season as food availability changed (Chavez-Ramirez 1996). To date, no whooping crane studies have explicitly considered foraging efficiency in relation to habitat use at the breeding grounds. In this study, we made use of video footage of 2 pairs of whooping cranes, collected for a study of whooping crane food intake (Fitzpatrick 2016),

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to develop methods and conduct a preliminary analysis of relationships between foraging habitat use, foraging rates, and foraging efficiencies for breeding EMP cranes in 2 habitat types: wetlands and agricultural fields.

We generated several alternate hypotheses regarding the relationship between crane habitat use and foraging efficiency during the breeding season, including the pre-nesting, incubation, and post-abandonment periods. We developed these hypotheses with the expectation that cranes would use wetlands more frequently than agricultural fields during pre-nesting and incubation periods and use agricultural fields more frequently following nest abandonment, as observed in previous studies (Van Schmidt et al. 2014, Fitzpatrick 2016). First, based on Chavez-Ramirez's (1996) findings with wintering AWBP cranes, we generated the simple hypothesis (H_1) that breeding cranes would spend more time in the habitat type (wetland vs. agricultural field) in which they were able to obtain higher foraging efficiency in order to achieve greater overall food consumption during each period of the breeding season.

However, factors besides adult foraging efficiency affect crane habitat use during the nesting season. Whooping Cranes nest in wetlands and likely choose territories based on a variety of needs, including nest sites and brood-rearing habitat that are safe from predators and provide food resources for chicks. Food resources for chicks, whose nutritional needs differ from those of adults (Wellington et al. 1996), are also important and may not peak until later in the season. Specific adult nutritional needs, such as the need to acquire protein and calcium for egg formation during the pre-nesting period, may also impact foraging habitat choice. Thus, during the pre-nesting period (H_2) and the post-abandonment period (for pairs preparing to renest) (H_3), adults may spend time in wetlands to engage in territory defense and nest-building or forage for specific nutrients, even if foraging efficiency on a general per-item basis is higher in agricultural fields. Similarly, during the incubation period when parents take turns incubating eggs, the non-incubating adult may choose to remain on territory to engage in territory defense, nest/mate protection, or communication about nest exchange timing, even if foraging efficiency is higher in agricultural fields (H_4). We note that few EMP whooping cranes have been observed to leave territories and forage in agricultural fields between nest exchanges (also Fitzpatrick 2016). Finally, avoidance of black flies post-nest abandonment may

lead cranes to forage in agricultural fields, even if foraging efficiencies are higher in wetlands (H_5). In general, endogenous reserves stored by adults may contribute to an ability to spend time in less efficient foraging habitats where trade-offs exist.

In this preliminary study, we collected data on 2 pairs of whooping cranes during the breeding season (pre-nesting, incubation, and post-abandonment) and measured stepping rates (i.e., steps per minute), a measure of foraging effort to encounter prey (Chavez-Ramirez 1996, Greer 2010); striking efficiency (number of food items captured per number of food acquisition attempts), a measure of foraging efficiency once prey is located (Hafner et al. 1982, Dimaxelis et al. 1997, Kent 1987); and overall ingestion rate (i.e., prey items swallowed per minute). Lower stepping rates, higher striking efficiency, and higher ingestion rates (hereafter called "capture rates") were considered more efficient.

STUDY AREA

Two pairs of cranes were observed on their breeding territories for this study, at Necedah National Wildlife Refuge (NWR) and on private property in Wood County, Wisconsin (Fig. 1). The 177-km² Necedah NWR consisted of open water, emergent herbaceous wetlands dominated by sedges (*Carex* spp.), and shrubby wetlands interspersed with mixed forest, shrub communities, and graminoid communities in uplands (Van Schmidt et al. 2014, Urbanek et al. 2018). Habitats around Necedah NWR include forests, agricultural fields, pastures, and cranberry bogs (Van Schmidt et al. 2014). The second location was a cranberry reservoir, located approximately 40 km northeast of Necedah NWR in Wood County (Fig. 1), and consisted of approximately 0.6 km² of open water and emergent herbaceous wetlands dominated by cattail (*Typha* spp.), interspersed with berms, and surrounded by forest (~10 km²). The forested area was surrounded primarily by agricultural fields, cranberry bogs, pastures, with some additional forest.

METHODS

Focal Birds

This preliminary study of breeding season foraging efficiency focused on 2 pairs of whooping cranes, observed during the 2013 breeding season

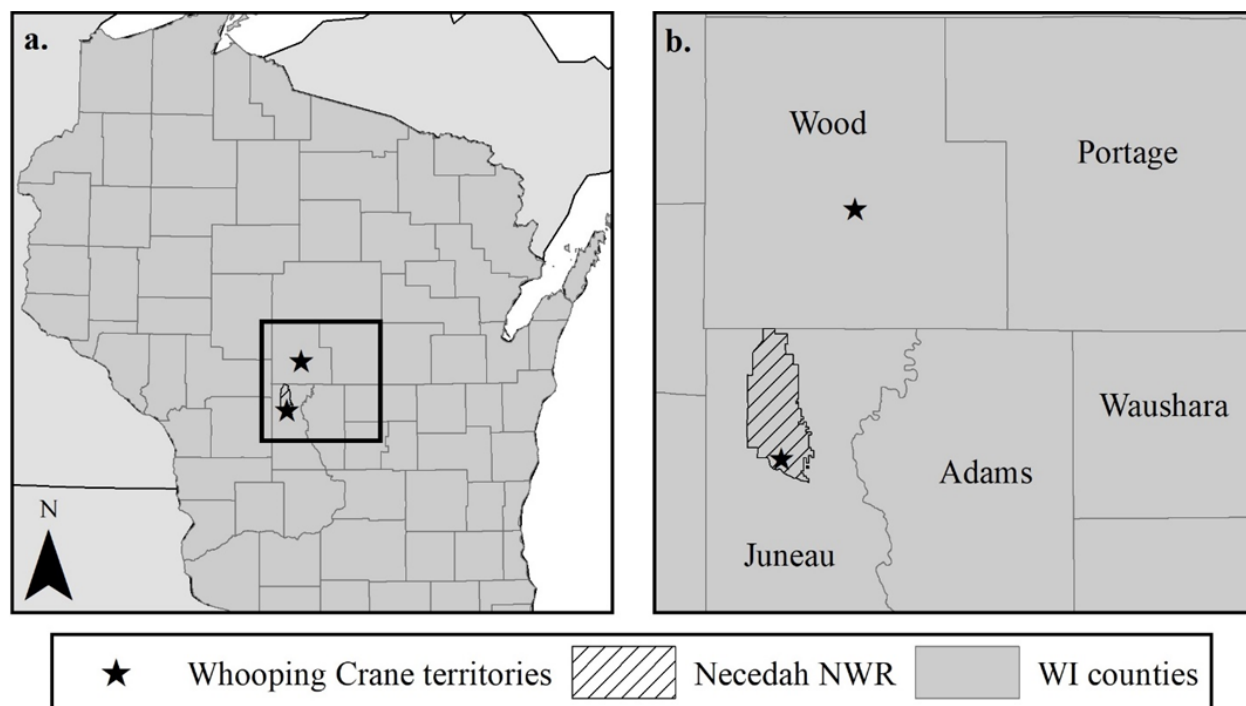


Figure 1. (a) Map of state of Wisconsin with county boundaries and an extent indicator for inset map (b) showing locations of nesting sites of 2 whooping crane pairs studied in Juneau (Necedah National Wildlife Refuge) and Wood Counties, 2013.

during 3 periods (pre-nesting, incubation, and post-abandonment). Both pairs abandoned their initial nesting attempts during incubation and did not re-nest. The timing of incubation for these 2 pairs was similar to that of other pairs in the population. These pairs were selected based on their tendency in previous years to spend time in areas that were visible from roads or potential blind locations. All birds hatched in captivity and were uniquely color-banded with the addition of VHF radio-transmitters for identification and location purposes (Advanced Telemetry Systems, Isanti, MN, USA), but transmitters of 1 pair were non-functional. Pairs were located by use of radio-telemetry with scanner receivers (Telonics, Mesa, AZ, USA) or by monitoring known breeding territories. One pair (13-02 and 18-02; bird order-hatch year) nested at Necedah NWR and incubated from 28 April to 4 May 2013. The 50% kernel density core home range size of the pair at Necedah NWR was approximately 0.4 km² and the 95% annual home range estimate was 3.9 km². The core area was completely within the refuge and surrounded the pair's nest site. The 95% home range included agricultural areas, typically corn stubble fields, approximately 17 km to the southwest

of the refuge, often used by the pair during the post-abandonment period. The other pair (12-02 and 19-04) nested in a cranberry reservoir on private property and incubated from 15 April to 5 May 2013. This pair's 50% core home range (0.8 km²) was bimodal, part of which was in the cranberry reservoir and part of which was in cranberry beds and upland areas approximately 2.5 km northeast of the nest site. The 95% home range size of this pair was approximately 5.5 km², and included locations surrounding the core home range in adjacent wetlands and uplands, typically cornfields and pastures. Home range sizes for both pairs were calculated with the 'kernelUD' function in the 'adehabitatHR' package in R (Calenge 2006, R Core Team 2017).

Video Recording

Focal birds were video-recorded for a concurrent study (Fitzpatrick 2016), and we calculated measures of foraging efficiency from videos for this study. Observers recorded all videos from an elevated blind or vehicle at a distance of at least 100 m in order to minimize disturbance. Data collection began within 9

days of the pair's arrival to their territory in the spring. The video-recording equipment used consisted of a Panasonic HCV-700K camcorder with an Olympus TCON-17× telephoto conversion lens, mounted on a tripod or vehicle window mount. Videos were recorded in high definition (1080×1920 pixels) at 60 progressive frames per second. Total optical magnification (35-mm equivalent) for the system ranged from approximately 1 to 24×. Magnification was also possible by using the Intelligent Zoom function on the camera.

Video-recording sessions were stratified throughout the day and season. Each focal pair was observed during 4, 7-hour sessions per week, consisting of 2 morning sessions (0600-1300 hr) and 2 afternoon sessions (1300-2000 hr). Within each session, we video-recorded cranes every other hour (alternating with another type of data collection for the concurrent study). We randomly determined the hour in which we began video recording (first or second hour of the session). Video-recording during a given hour focused on 1 crane of the pair, and the focal bird (male vs. female) was alternated between video-hours within a 7-hour session. We also randomly selected which member of the pair we video-recorded first. The focal crane was recorded for a total of 50 minutes (or as much time as the bird was visible to the observer), starting at the beginning of the hour, to allow observers a 10-minute break between data collection sessions. For each hour of observation, we recorded the time, focal bird identification number, and location (latitude/longitude). Observers sometimes recorded cranes opportunistically in between video-hours if there was an especially clear view of a foraging crane and data for the concurrent study could be collected simultaneously. For the purposes of this study, we also opportunistically collected data on non-focal cranes in the videos if they were visible within the frame.

During the incubation period, observations were limited to 2 sessions (1 morning, 1 afternoon) per week to reduce disturbance, and video recording always focused on the off-nest bird. Data during this period were collected exclusively from the Wood County pair because the Juneau County pair nested in such close proximity to the blind that it could not be accessed without disturbing the nest. This latter pair was also not generally visible from the road when on its territory. Due to this limited sample, we discuss data from the incubation period as preliminary and a demonstration of the type of data that could be collected to further investigate foraging metrics during this period.

Data Collection from Videos

We collected data from videos from 7 April through 5 June 2013. We recorded habitat type and all measures of foraging effort and success during times when cranes were visible in videos. We classified habitat into 3 main types, agricultural, wetland, and other, by grouping National Land Cover Database (Homer et al. 2015) land cover categories (agriculture: cultivated crops and pasture; wetland: emergent herbaceous wetland and open water; other: all other used land cover categories not included in agriculture or wetland). Most agricultural fields used by cranes in this study were corn or soybean stubble when data collection began, were planted in early May, and had crops growing by the end of the data collection period. When cranes moved between habitat types, we recorded the change and collected behavior data separately for each habitat type. Behavior bouts (hereafter bouts) were considered discrete when a bird exhibited a different behavior, was out of sight for more than 10 seconds, or changed habitat type. To calculate percent of time in each habitat type, we calculated the amount of time cranes were in each habitat type and divided by the total amount of time cranes were visible in videos, separately by period of the nesting season.

For each 50-minute video session, we measured the time spent foraging. Foraging bouts were defined as periods of 10 seconds or more when cranes were visible and exhibiting any food searching or acquisition behavior. Behaviors were based on crane ethnography defined by Masatomi and Kitigawa (1975) and Ellis et al. (1991) and used by Fitzpatrick (2016) and Barzen et al. (2018*d*). We identified food searching behavior when cranes explored the ground, water, or vegetation while stationary or walking, typically with a horizontal body position and the head down, near the ground (Masatomi and Kitigawa 1975). Food acquisition behaviors were usually probes, jabs, or stabs as defined in Barzen et al. (2018*d*). When cranes spent less than 10 seconds exhibiting other behaviors within bouts, we subtracted that time from the total time spent foraging during that bout. To maintain data quality, we did not use videos when cranes were out of focus due to weather, habitat, camera shake, or other factors.

During foraging bouts, we counted the number of steps, the number of unsuccessful (strikes), and successful (captures) food acquisition attempts. Captures were determined by a distinctive head jerking motion used to swallow food items (Barzen

et al. 2018d). For each 50-minute video session, we calculated the total time spent in foraging bouts in both wetland and agricultural habitat types. Foraging bouts varied in duration, so we standardized all foraging rates to be per minute spent foraging during the 50-minute video session. For example, we calculated food capture rates as total number of captures during all foraging bouts in the 50-minute video session divided by total time spent foraging during that session. Additionally, we calculated the stepping rate by dividing the total number of steps by total time spent in foraging bouts during the video session. Lastly, we used the number of strikes and captures in the video to calculate striking efficiency as number of captures/(number of captures + strikes).

Data Analysis

We combined observations from the 4 birds for analysis of these data. We recognize individuals in a pair do not move independently while active in the same territory. However, during incubation we focused on the off-nest individual, whose behaviors would be independent of its mate. We did not include time spent in “other” habitat for any analyses because very few observations of cranes were recorded in these habitats. For all analyses, *P*-values were considered significant with $\alpha < 0.05$.

For all behaviors, we compared the percentage of time spent in agriculture and wetland habitats during all 3 periods of the reproductive cycle (pre-nesting, incubation, post-abandonment) using a chi-square test in the statistical program R (R Core Team 2017). No time spent out of sight was included in analyses to ensure correct habitat assignment. We used a post-hoc test in the ‘fifer package’ in R to determine differences in habitat use between periods (Fife 2014, R Core Team 2017).

We used generalized linear models to analyze the effects of habitat and period for each measure of foraging behavior. Response variables were stepping rate, striking efficiency, and capture rate (1 value for each habitat type per 50-min video). We determined the distribution of all response variables using quantile-comparison plots with the ‘car package’ in R (Fox and Weisberg 2011, R Core Team 2017). Stepping rate and striking efficiency best fit a normal distribution. However, capture rates best fit a log-normal distribution, so we added 0.1 to each capture rate to have non-zero values that were possible to log-transform. We then used

a penalized quasi-likelihood generalized linear mixed model, which is a flexible technique suitable for normal and non-normal data, using the ‘MASS package’ in R (Venables and Ripley 2002, R Core Team 2017).

We analyzed data separately by period to assess the influence of habitat on each response variable during each period. For each analysis, bird ID was used as a random effect, while habitat was used as a fixed effect. We then pooled data from all periods and included period in the model as a fixed effect to determine if there were differences in foraging rates throughout the breeding season. We identified a correlation between habitat and period with a chi-square test, thus they were tested separately in the models ($P < 0.05$, R Core Team 2017).

RESULTS

We observed 419 video segments, which consisted of a total of 122.8 hours of video. When both cranes were visible in the frame, we collected data on both birds, resulting in a total of 218.6 bird-hours of video. If cranes were not found during part of the 50-minute video session, video segments were shorter than the full 50-minute session ($\bar{x} = 14.0 \pm 0.5$ min). Of the 419 total video segments, 269 segments contained foraging bouts of 1 or both birds, resulting in 416 bird-video segments. Of the 218.6 bird-hours of video observed, approximately 39.1 hours consisted of foraging bouts. All measurements reported below are standardized rates calculated from bird-video segments, so there is 1 value representing each bird in each video segment containing foraging bouts. Foraging bouts represented in bird-videos were on average 5.6 ± 0.3 minutes in duration, and all rates reported here were standardized by minute. The majority of bird-videos collected for this study were during the post-abandonment period ($n = 191$ and 113 bird-videos, for agriculture and wetlands, respectively, Fig. 2). We had smaller sample sizes during the pre-nesting ($n = 13$ and 78 bird-videos, for agriculture and wetlands, respectively) and incubation periods ($n = 3$ and 18 bird-videos, for agriculture and wetlands, respectively, Fig. 2).

Habitat Use

Time that cranes spent in agriculture versus wetland habitats differed between periods ($\chi^2_2 = 20.5$, $P < 0.001$). Cranes used wetland habitats more than agricultural habitats during pre-nesting (84.1%) compared to the

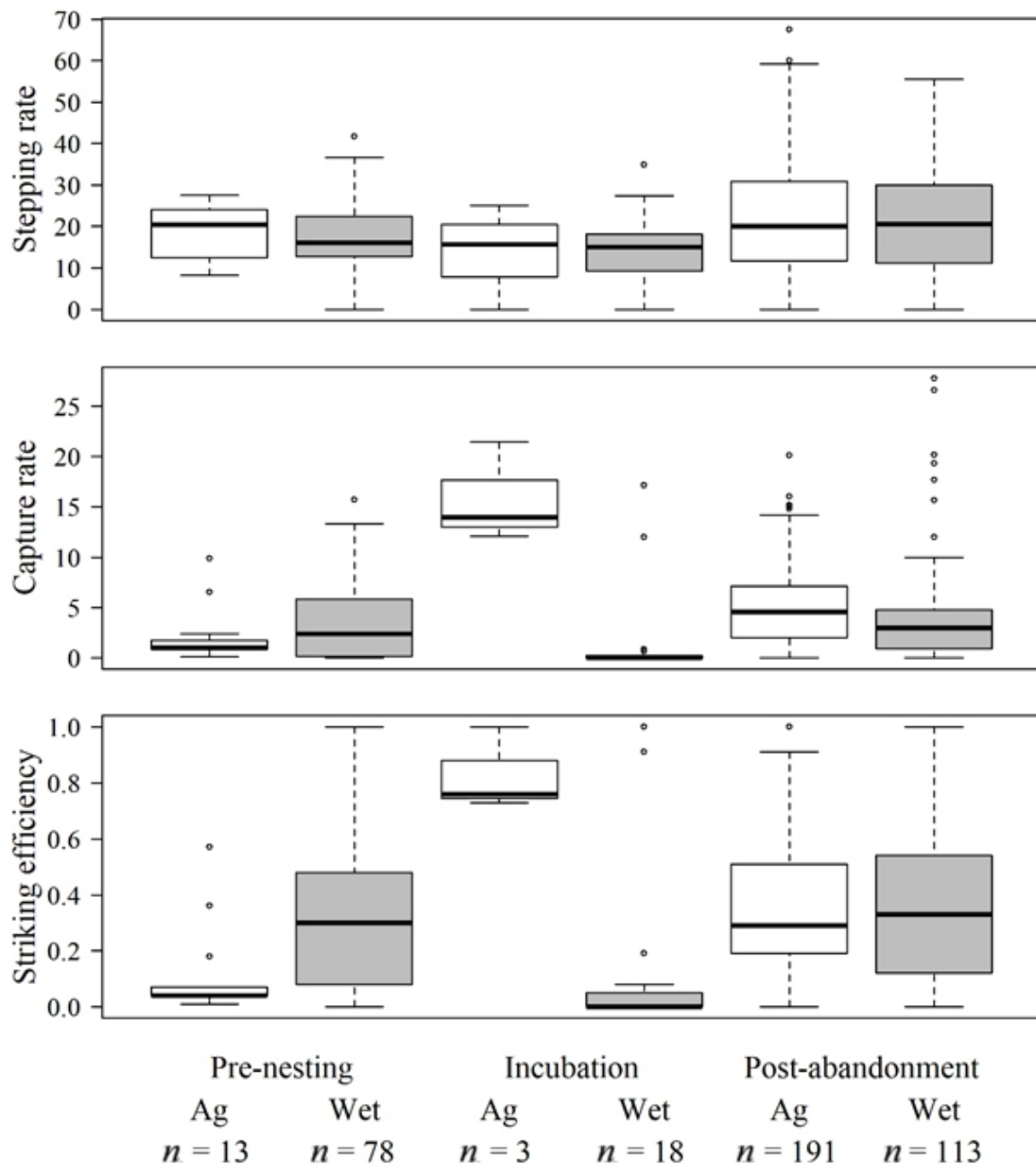


Figure 2. (Top) Stepping rates (steps/min during foraging bouts), (middle) capture rates (captures/min during foraging bouts), and (bottom) striking efficiencies (no. captures/(no. captures + no. attempts)) for 2 pairs of breeding whooping cranes in agricultural (Ag) and wetland (Wet) habitats of central Wisconsin in 2013. Dark horizontal bars represent the median. Fifty percent of the data are within the box, and the other 50% are within the whiskers; open circles represent outliers. Sample sizes (n) are standardized measurements of foraging behaviors calculated in each habitat type during all foraging bouts in each bird-video.

post-abandonment period (37.8%, $P < 0.001$). Crane use of wetland habitats did not differ between pre-nesting and incubation periods (88.1% during incubation, $P > 0.999$), nor between incubation and post-abandonment periods ($P = 0.231$).

Measures of Foraging Effort and Success

We first modeled the relationship between habitat and foraging effort or success separately for each period. Whooping crane stepping rates in agriculture

and wetland habitats during each period did not vary ($P > 0.5$ for all analyses, Fig. 2). Capture rates were also similar in agriculture and wetland habitats during the pre-nesting and post-abandonment periods ($P > 0.1$ for both analyses, Fig. 2) but dissimilar during the incubation period ($P = 0.003$, Fig. 2). In contrast, whooping cranes had higher striking efficiency in wetlands during the pre-nesting period ($P = 0.049$), and higher striking efficiency in agriculture during incubation ($P = 0.001$, Fig. 2). Striking efficiency did not differ between agriculture and wetlands during the post-abandonment period ($P = 0.848$, Fig. 2).

When we pooled all data, stepping rates of whooping cranes were affected by both habitat and period ($P = 0.031$ and $P = 0.001$, respectively). With data pooled across periods, cranes had lower stepping rates in wetlands (19.2 ± 0.8 steps/min) than in agricultural fields (21.6 ± 0.9 steps/min, $P = 0.031$). With data pooled across habitats, whooping cranes had higher stepping rates during the post-abandonment period (21.8 ± 0.8 steps/min) than during incubation (14.5 ± 2.0 steps/min) or pre-nesting (17.2 ± 0.9 steps/min, $P = 0.010$ and $P = 0.002$, respectively), and there was no difference between incubation and pre-nesting periods ($P = 0.369$). The average stepping rate during all periods and in both habitats was 20.4 ± 0.6 steps/minute.

Overall, striking efficiency was unaffected by habitat ($P = 0.398$) but was different by period ($P = 0.021$). Striking efficiencies were higher during post-abandonment (0.4 ± 0.01 successes/attempt) than during pre-nesting (0.3 ± 0.03 successes/attempt, $P = 0.011$), but the incubation period (0.2 ± 0.08 successes/attempt) was no different than pre-nesting nor post-abandonment periods ($P = 0.771$ and $P = 0.093$, respectively). The average striking efficiency during all periods and in both habitats was 0.3 ± 0.01 successes/attempt. Lastly, during the overall breeding season, habitat and period had an effect on whooping crane food capture rates ($P = 0.003$ and $P = 0.046$, respectively). Whooping cranes consumed more food items per minute in agricultural habitats than in wetlands ($\bar{x} = 4.9 \pm 0.3$ items/min and 3.7 ± 0.3 items/min, respectively). Capture rates were higher in the post-abandonment period (4.6 ± 0.2 items/min) compared to pre-nesting (3.3 ± 0.4 items/min, $P = 0.030$), but cranes captured food at similar rates during incubation (3.8 ± 1.5 items/min) than during both pre-nesting and post-abandonment periods ($P = 0.679$ and $P = 0.438$, respectively). The average capture rates during all periods and in both habitats was 4.3 ± 0.2 items/minute.

DISCUSSION

Whooping cranes in this study spent more time in wetland habitats than agricultural habitats during the pre-nesting and incubation periods, but more time in agricultural habitat during the post-abandonment period. This pattern was expected based on results of previous studies (Fitzpatrick 2016, Van Schmidt et al 2014).

During the pre-nesting period, cranes exhibited higher striking efficiencies in wetlands, whereas stepping rates and capture rates during foraging bouts did not differ from agricultural habitats. This supports our hypothesis (H_1) that breeding cranes spend more time in the habitat type (wetland vs. agricultural field) in which they are able to obtain higher foraging efficiency in order to achieve greater overall food consumption. Higher striking efficiencies could reduce the amount of time and energy required to capture food items. However, we note that whooping cranes likely benefit from being able to more efficiently acquire food resources in the habitat type where they can also build nests and defend territory.

An important caveat to our results is that we measured foraging efficiency on a per-item basis, without considering the nutrient content per item (e.g., energy, protein, calcium). However, Fitzpatrick (2016) documented food types and sizes from the same set of videos. During the pre-nesting period, the most commonly consumed food items in wetlands were small snails and aquatic insect larvae, whereas earthworms were the only food items observed being consumed in agricultural fields during the pre-nesting period (Fitzpatrick 2016). It is possible that the energy obtained per food item in agricultural fields offset extra energy costs associated with lower striking efficiency. However, female cranes may also benefit from acquiring calcium from snail shells in wetlands prior to egg deposition.

During the incubation period, we observed non-incubating cranes most often in wetlands, but capture rates and striking efficiencies were higher in agricultural habitat. This supports our hypothesis (H_4) that the non-incubating adult choose to spend more time in wetlands to engage in territory defense, nest/mate protection, or communication about nest exchange timing, even if foraging efficiency is higher in agricultural fields. However, the fact that cranes traveled to agricultural fields at all suggests that there may be a trade-off between spending time in agricultural fields and wetlands during

incubation. Our results suggest that 1 benefit is more efficient foraging in agricultural fields, but we note that use of agricultural fields may also allow the off-nest parent to avoid black flies.

Data for the incubation period should be interpreted with caution because observations were limited to 1 pair of cranes, were almost exclusively obtained from wetland habitats, and at half the observation rate of the other 2 periods. Therefore, results are heavily influenced by the behaviors observed in wetlands from a single pair of cranes in Wood County. The wetlands at Necedah NWR are a part of a much larger complex of wetlands (177 km² total area) managed for various wildlife and habitat objectives, whereas the Wood County wetland is smaller (0.6 km² of open water and emergent wetland surrounded by forest), is primarily managed as a reservoir for water used in cranberry production, and lies in closer proximity to agricultural fields. Water levels at Necedah NWR and in Wood County are managed for different objectives (managing wildlife habitat vs. holding water for cranberry production), however both are impounded natural wetlands with emergent herbaceous vegetation. The cranberry reservoir in Wood County is not used for cranberry production during the course of the whooping crane breeding season, but holds water that is used to flood cranberry beds for harvest in fall.

After cranes had abandoned their nests, we observed them most often in agricultural areas. During this period, we did not see any differences in measures of foraging effort or success between agriculture and wetlands, suggesting that cranes may choose to use agricultural habitats at this time for another reason, e.g., black fly avoidance. However, we note that potential for energy intake may be higher in agricultural fields due to consumption of energy-rich waste corn (Fitzpatrick 2016, Barzen et al. 2018d).

With data from all periods pooled, cranes had higher stepping rates and food capture rates in agricultural habitats than in wetlands. The significance in pooled results, when most individual period results were not significant, is likely a result of a larger sample size. Stepping rates and capture rates were only slightly higher in agricultural than in wetland habitats. Whooping cranes also exhibited higher stepping rates or energy spent searching for food during the post-abandonment period, and higher striking efficiencies and capture rates compared to the pre-nesting period, when data were pooled across habitats. We suggest that these trends warrant further exploration with more pairs

of cranes. Given that stepping rates and food capture rates tended to increase together, we suggest that future studies use steps per food item captured as an additional measure of foraging efficiency.

Our measured values for stepping rates fell within the range of values that have been observed in AWBP cranes on their wintering grounds in coastal Texas. The average stepping rates of EMP whooping cranes in this study, 21.6 and 19.2 steps/minutes in agricultural fields and in wetlands, respectively (Fig. 2), were slightly higher than those observed by Greer (2010) (17.9-18.9 steps/min) in salt marsh habitats. Our values were lower than those observed by Chavez-Ramirez (1996) for wintering AWBP whooping cranes in salt marsh vegetation, where they primarily consumed wolfberries (*Lycium carolinianum*) (27.1-29.8 steps/min), but in the middle to upper end of values observed in other habitats: ranges 14.3-26.1 steps/minute in open water within salt marshes where the primary food was blue crabs (*Callinectes sapidus*), 7.9-24.1 steps/minute in bays where the primary food was dwarf and razor clams (*Mulinia lateralis* and *Tagelus plebeius*), and 10.4-27.1 steps/minute in uplands following prescribed burns where the primary foods were dead or dying insects and small reptiles. Overall, comparable stepping rates suggest that the 2 populations exhibit similar levels of locomotive effort to find food at the 2 locations, although we note that a summering and wintering location are not directly comparable.

Average capture rates in this study (4.9 items/min in agricultural fields and 3.7 items/min in wetlands) were also similar to those observed for wolfberries by both Greer (2010) (1.4-5.1 items/min) and Chavez-Ramirez (1996) (2.3-3.9 items/min) and faster than values (items/min) observed for other types of food, including 0.05-0.1 for blue crabs and 0.2 for razor clams (Chavez-Ramirez 1996) and 0.01-0.06 for blue crabs, 0.2 for clams, 0.05-1.2 for snails, and 0.3 for insects (Greer 2010), but slower than those observed for dwarf clams (10.9 items/min, Chavez-Ramirez 1996). Relatively fast capture rates may be reflective of the small size and minimal handling time required for the most common food items consumed by whooping cranes in this study (snails, aquatic insect larvae, earthworms, corn), in addition to food availability. However, capture rates were slower than those of greater sandhill cranes (*Grus canadensis tabida*) in cornfields near Briggsville, Wisconsin, in spring (6.08 items/min) (Barzen et al. 2018b). This difference could occur because whooping cranes are less efficient foragers in agricultural fields

than sandhill cranes, or because food availability was lower at our study location and later in the year.

In conclusion, our preliminary data indicate that cranes spend most time in the habitat type where they achieve the highest foraging efficiency on a per-item basis during the pre-nesting period (wetlands), but not during the incubation period (agricultural fields) or post-nesting period (no difference between wetlands and agricultural fields). Our results are preliminary because they are based on 2 crane pairs observed in only 1 year, and we obtained limited data during incubation. Moreover, observations of all birds were compiled with the assumption that the measured parameters would not differ between individuals. Male and female birds or specific pairs could display differences in foraging behavior and efficiency. The territories of the focal pairs for this study represent 2 types of habitat used by whooping cranes in the EMP (a protected wetland complex at Necedah NWR and a privately-owned wetland used to hold water for cranberry production), but are not representative of all types of nesting habitat used by this population. One important aspect that was not considered for this study was the distance traveled between nesting wetland sites and agricultural foraging sites. Whether cranes required a short or long-distance flight to reach suitable foraging habitat could also have an impact on patch choice and energetic costs of foraging.

We suggest future studies consider multiple variables such as pre-nesting body condition, territory quality, suitable patch distance, food item sampling on foraging grounds, and the spatio-temporal dynamics of prey availability. Combined with type and size of prey, capture rates, and striking efficiency, such data would be meaningful parameters in future studies of foraging energetics (Dimaxelis et al. 1997). By better understanding the importance of both wetlands and agricultural areas for foraging before, during, and after the breeding season, outcomes of this study can benefit the reintroduction and management strategies for this species, and specifically help us better understand habitat needs in the Eastern Migratory Population.

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